Tansley review

Biological control of invasive plant species: a reassessment for the Anthropocene

Author for correspondence:
Timothy R. Seastedt
Tel: +1 303 492 6387
Email: timothy.seastedt@colorado.edu
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Summary

The science of finding, testing and releasing herbivores and pathogens to control invasive plant species has achieved a level of maturity and success that argues for continued and expanded use of this program. The practice, however, remains unpopular with some conservationists, invasion biologists, and stakeholders. The ecological and economic benefits of controlling densities of problematic plant species using biological control agents can be quantified, but the risks and net benefits of biological control programs are often derived from social or cultural rather than scientific criteria. Management of invasive plants is a 'wicked problem', and local outcomes to wicked problems have both positive and negative consequences differentially affecting various groups of stakeholders. The program has inherent uncertainties; inserting species into communities that are experiencing directional or even transformational changes can produce multiple outcomes due to context-specific factors that are further confounded by environmental change drivers. Despite these uncertainties, biological control could play a larger role in mitigation and adaptation strategies used to maintain biological diversity as well as contribute to human well-being by protecting food and fiber resources.

I. Introduction

Invasion science involves the study and management of organisms introduced outside their native range (Richardson et al., 2011; Kuéffler et al., 2013). The fact that some of these introduced species affect the abundances and presence of other species and may have substantial economic impacts is without dispute. Within the framework of invasion biology, the practice of searching for, testing, and releasing biological control agents designed to reduce negative impacts of invasive plants is an established science. This program has been heavily scrutinized and has a documented record of success with a remarkably low rate of nontarget effects and other unintended consequences (Müller-Schärer & Schaffner, 2008; Clewley et al., 2012; Julien et al., 2012; van Wilgen et al., 2013; Suckling & Sforza, 2014). Cost–benefit analyses of biological control programs usually show an overwhelming economic
justification for the use of biological control agents (De Clercq et al., 2011). That said, biological control programs appear underutilized and continue to be viewed with skepticism by some ecologists and conservationists (Fowler et al., 2012; Simberloff, 2012). Nonetheless, substantial progress in resolving real and perceived problems associated with biological control has been made in recent decades, and success stories of biological control continue to emerge from efforts begun decades ago.

To some natural and social scientists, invasion biology lacks a unified scientific framework and agenda because of different conceptual understandings, uncertainties that are unlikely to be substantially reduced, missing empirical information, and differences in value judgments associated with risk and cost–benefit assessments (Hattingh, 2011; Barney et al., 2013; Humair et al., 2014). The application of biological agents to control invasive plant species is seen by some to suffer from similar issues. Monitoring efforts for biological control releases often remain unfunded or nonexistent, and successful science is slow to be transferred into management protocols because of communication lags between scientists and managers (Shaw et al., 2010; Matzek et al., 2014). An emerging, confounding issue is that, under the altered and changing environmental conditions of the 21st Century, plants targeted for biological control programs decades ago now are desirable to a subset of stakeholders because of the ecosystem or conservation services these plants provide (e.g. Sher, 2013). Native plants might have provided those services in the past, but directional environmental changes or human disturbances in addition to the plant invasions may now preclude or greatly limit those contributions. The science and practice of biological control remains underappreciated because of these issues, in addition to the lack of a strong consensus from the scientific community.

This Tansley review is written from the perspective of a terrestrial ecosystem ecologist involved in both studies and management of invasive plant species. I briefly review the science that drives the application of biological control agents as a management tool for invasive plant species. I identify uncertainties that limit the ability of biological control procedures to provide a single tool that solves most invasive plant species problems. I then evaluate how the efficacies of biological control efforts are influenced and altered by environmental sensitivity to other control options such as environmental changes, the new normal for the Anthropocene, will impact the outcomes, benefits and risks of biological control programs.

Classical biological control can be viewed as proactive attempts to manipulate food webs to restructure a biotic community in ways that enhance ecosystem services, including conservation goals and human welfare. A broader view of biological control within the context of invasive species management can be found in Van Driesche et al. (2008), Clout & Williams (2009), Davis (2009), and Lockwood et al. (2013). While biological control of undesirable plants and plant pests in croplands is an active area of research
(Seastedt, 2014), the focus here is on biological control of invasive plants in rangelands, shrublands and forests, primarily by herbivores.

III. Trajectories of biological control efforts

Three case studies are presented here to suggest that biological control efforts often follow similar trajectories (c.f. Briese, 2004; Evans, 2013). In general, to initiate a biological control effort, a plant species is acknowledged as being in need of control. Eradication over the entire introduced range is viewed as unlikely, and control by mechanical removal and herbicides, alone, is recognized as impractical and unsustainable. The evolution of herbicide resistance by problematic invasive species has increased the relative benefits of using biological control (Evans, 2013). Such decisions are bolstered by cost–benefit analyses suggesting substantial value in pursuing the management activity. Then the search for testing and releasing of biological control agents is undertaken, and that phase continues should first attempts be judged inadequate or insufficient. Finally, the outcome of the interaction is viewed through both scientific and social filters, identifying both the metrics and consequences of successes and limitations.

1. Case study 1: saltceder or tamarisk (Tamarix spp.) invasions into North America

Several species of Tamarix, riparian trees and shrubs from Eurasia, were brought into North America and deliberately planted as ornamentals and used in erosion control during the 19th Century. These trees and shrubs then colonized riparian areas, primarily throughout the southwestern regions of North America, often forming dense, almost impenetrable monocultures along rivers and streams. Two species were common (Tamarix ramosissima and Tamarix chinensis) and these subsequently hybridized (Sher, 2013). By the late 20th Century, these species had been reported in newspapers to be ‘a water gulping, fire feeding, habitat ruining, saltspreading monster’ (Chew, 2013, p. 269–270). Zavaleta (2000) indicated that control costs were more than justified given these impacts. Studies on this invasive plant group, including measurements of the ecology, impacts, and economic damage caused by these species in their introduced habitats, resulted in over 200 publications in about a 40-yr period (Stromberg et al., 2012). A major synthesis summarizing the ecological, economic, and sociological dimensions of the tamarisk invasion was produced in 2013 (Sher & Quigley, 2013).

The biological control efforts for tamarisk began in the 1960s (Sogg et al., 2013). Several species of Diorhabda beetles (Chrysomelidae) obtained from Asia were field tested beginning in the 1990s, with caged releases in 1997–2000, and open releases in 2001 (Bean et al., 2013). Defoliations of tamarisk by these biological control agents were observed by 2002, and major diebacks of tamarisk were noted in many areas in subsequent years (Bean et al., 2013). For now, there is substantial evidence that sustainable control of tamarisk populations by these and other biological control insects will be achieved across much if not most of the plants’ introduced range. That judgment may need to be modified if continued hybridization of the tamarisk species in North America alters the plant’s response to biological control agents (Williams et al., 2014).

The use of biological control agents for Tamarix spp. was complicated by the recognition of important ecosystem services provided by these introduced plants. The tree provides nesting habitat for an endangered bird, the southwestern willow flycatcher (Empidonax traillii extimus). Release of biological control agents was delayed while this problem was evaluated, and the government release program was terminated in 2010 as a result of concerns for the endangered species. As the biological control agent was already established by 2010, this action would likely have little long-term effect, and the consequences of biocontrol releases for the bird species remain under study (Sher, 2013). In addition to these concerns, the use of tamarisk species for erosion control and questions about what will replace this species when greatly reduced by the insects and other control methods have resulted in second thoughts about its removal (Hulthine et al., 2010; Dudley & Bean, 2012; Sher, 2013). While all authors agree that restoration using native species is the desirable solution, Sher (2013) notes that there are multiple reasons to believe that this is an unrealistic expectation. The fact that most riparian zones in this region of North America have regulated flows as a result of water storage for cities and agriculture implies that these areas will not assume their historic vegetation composition, regardless of the presence or absence of tamarisk.

2. Case study 2: knapweed (Centaurea spp.) invasions in North America

The North American grasslands and rangelands have been invaded by invasive trees, shrubs, forbs, and grasses, with most of the introductions and invasions occurring during the period of 1850–1940. Among these, several species of Centaurea (Asteraceae) caused widespread economic and ecological damage. These species were among those identified for biological control, with most studies initiated in the 1960s and 1970s (Müller-Schärer & Schroeder, 1993). A report in the well-respected Smithsonian Magazine singled out a Centaurea species and declared, ‘Spotted knapweed is driving out native plants and destroying rangeland, costing ranchers millions. Can anybody stop this outlaw?’ (Alper, 2004, p. 33). Similar to tamarisk, economic concerns (this time focusing on forage rather than water) appeared to drive the need for control.

Müller-Schärer & Schroeder (1993) evaluated the status of biological control efforts for Centaurea in North America and asked the question, ‘Do insects solve the problem? The authors focused on two species, spotted knapweed (Centaurea stoebe) and diffuse knapweed (Centaurea diffusa). At the time of the Müller-Schärer & Schroeder (1993) publication, no reductions in Centaurea species densities had been reported as a result of releases of over a dozen species of introduced biological control insects, several of which were released in the 1970s. These insects established on the host species, but appeared to alter food webs more than they influenced target plant abundance.
In the two Centaurea species, the production of strong putative allelopathic substances was reported, that is, the exudation of chemicals from root tissues to harm adjacent, competing plant species, which potentially could be amplified by biological control agents (Thelen et al., 2005). Field mice were reported to feed upon several of the knapweed biological control agents, and as a consequence to show an increase in their populations. The mice also ate seeds of competing plant species, and carried the human disease hantavirus (Pearson & Callaway, 2006). Thus, biological controls for knapweed species were identified (1) to increase positive feedbacks to the invasive plant through soil microbial or chemical pathways, (2) to alter food webs (enhancing the abundance of generalist omnivores) in ways that also indirectly benefited the invasive plant by reducing plant competition, and (3) to alter food webs in ways that contributed to a potentially fatal human disease.

Soon thereafter, however, declines in knapweed densities as a result of biological control activity were reported by management agencies as well as by Story et al. (2006, 2008). By 2010, the allelopathic characteristics attributed to Centaurea spp. were disputed and retracted, as was the possible amplification effect of biological control agents (Norton et al., 2008; Duke, 2010). The biological control agents for these species were largely absolved of their unintended consequences.

Two weevil species, a seed-head feeder, Larinus minutus, and a root-feeder, Cyphocleonus achates (both Curculionidae; Fig. 1), listed among the 14 insect species suggested as potential biological control agents by Müller-Schärer & Schroeder (1993), were subsequently confirmed to greatly reduce densities of C. diffusa (Myers et al., 2009; Gayton & Miller, 2012). Reports indicated similar control of C. stoebe by the same weevils, with declines observed in monitored field populations of spotted knapweed (Story et al., 2008; Knochel et al., 2010; Gayton & Miller, 2012). Not all experimental studies have confirmed this result (Ortega et al., 2012), and some concern remains that the plant species may still be capable of persisting in unacceptable densities in a subset of habitats in spite of the presence of these biological control agents (Maines et al., 2013).

The success of biological control for these two knapweed species has caused consternation among a subset of stakeholders. Early on, knapweeds had been identified as important to the honey industry in North America (Maddox et al., 1985). While native pollinators still appear to be most benefited by native flowering plants, focus on the health of honeybees and the success of commercial pollination activities has increased in importance (Carson, 2013). Societal pressure to restrain or reduce biological control efforts against knapweed is therefore part of the ongoing management dialog in parts of North America.

3. Case study 3: nodding thistle invasions into North America, Australia, and New Zealand

Nodding thistle, Carduus nutans (Asteraceae), a monocarpic, annual or biennial species of Eurasian origin, was introduced into North America c. 170 yr ago, and introduced into New Zealand in c. 1900 and into Australia in the 1940s. It is also a concern in South America and has been identified as an invasive plant species in South Africa. This species degrades grazing lands and has invaded temperate zone, humid to semiarid plant communities throughout the world.

The nodding thistle is constrained in at least a portion of its home range by herbivores (Jongejans et al., 2006); thus it was a logical target for classical biological control. Gassmann & Kok (2002) reported that this species was among the first group selected for biological control by the US Department of Agriculture in 1959, and in 1968 the weevil Rhinocyllus conicus (Curculionidae) was released in the USA, followed by releases in Canada in 1969. The species was introduced in New Zealand in 1972 and in Australia in 1985 (Cullen & Sheppard, 2012). What subsequently happened in North America is a well-known story. Rhinocyllus conicus attacked native thistle species of North America. In the 1960s, this threat to native species was not considered sufficient to negate the potential benefit of the biological control program, and the insects were subsequently released. By the 1980s, concern about the lack of host specificity and damage to native thistles was identified, but it was not until 2000 that the US Department of Agriculture banned interstate shipments of this biological control agent (Louda et al., 2003). The weevil is well established and is viewed as a threat to the persistence of at least some North American thistles (e.g. Rose et al., 2005). This biological control program was the model system for redefining the ethics and risk identified for subsequent biological control efforts (Fowler et al., 2000; Delfosse, 2005).

Attempts to control nodding thistle continued after the release of R. conicus with the introduction of five other insect species released in North America (Gassmann & Kok, 2002), with two additional species released in New Zealand and Australia (Cullen & Sheppard, 2006).
In contrast to what occurred in North America, lessons learned from the nodding thistle—biological control interactions in New Zealand and Australia were of a different sort. As there were no native thistle species in those countries that were close relatives to the introduced plants, concerns regarding direct nontarget effects were minimized. Instead, the focus was on factors influencing the efficacy of the plant–biological control interactions. These studies have contributed substantially to our understanding of the thistle–insect interactions as a model system for understanding how biological control can vary over space and time, and these findings are discussed in sections below.

IV. Current research

1. Can we consistently predict the outcome of biological control introductions?

Perhaps one generalization that has remained consistent over recent decades is that the impacts or efficacies of biological control agents are usually context specific, as seen in the case of C. stoebe described above (in Section III.2), and in the nodding thistle (Shea et al., 2005). In New Zealand, the populations of nodding thistle are short-lived and rely on large amounts of seed production for rapid population growth. In Australian populations, seed production of C. nutans is of less concern and survivorship of rosettes is more important to population dynamics (Shea et al., 2005). Thus, insects that reduced seed production became key control agents in New Zealand, while insects that attacked immature growth forms, the rosettes, were more important in Australia. The rich history of studies of plant–herbivore interactions over their biogeographic ranges provides the conceptual framework for this phenomenon for both native and introduced plant species (Lau et al., 2008 and references therein; Shea et al., 2010). While the magnitude and direction of interactions can vary among native and introduced habitats, the outcome is determined by the net impact on plant fitness within the introduced community (Fig. 2).

Myers & Bazely (2003) presented a conceptual framework that suggests why an effective herbivore or pathogen under one set of abiotic and biotic constraints may fail to be effective under different constraints, and why, sometimes, this might allow for the selection of inferior biological control agents. The presence or absence of predators controlling the abundance of the biological control agents at one site but not at the other would be sufficient to produce a context-specific outcome. Soil nutrients appear to be another variable affecting this outcome (Jamieson et al., 2012a; Hovick & Carson, 2014). Thus, both ‘top-down’ (e.g. predation) and ‘bottom-up’ (e.g. resources, potentially mediated by competition) factors affect the plant–consumer interaction. Is a biological control ‘weak’ in terms of its effect on plant fitness in its native habitat because of the coevolved interactions between the plant and herbivore, or is this weakness imposed by other factors that limit the abundance of the control? If the latter is true, how then will the dynamics change in the introduced environment? Selecting the ‘best’ control agent is not easy. In the case study of the knapweed species, the most successful biological control agents were weevils which were not introduced into North America until c. 20 yr after the first biological control agents were released. Similarly, a more effective biological control agent for nodding thistle in New Zealand was introduced 20 yr after the release of the initial biological control agent (Groeneman et al., 2007).

2. Biological control agents and population dynamics

Individual plants can undercompensate, compensate, or rarely overcompensate when attacked by herbivores (McNaughton, 1979; Wise & Abrahamson, 2007). What this means is that relative growth rates can decrease, remain unchanged or increase such that plant productivity (and, in some cases, direct measurements of fitness) can decrease, remain unchanged, or increase. While the individual responses are important in understanding biological control efforts, population-level responses (as measured by numbers, biomass, or seed production per species per unit area) tend to commonly drive the assessment of plant–biological control agent interactions. Plants can exhibit population-level compensatory responses to seed reduction (e.g. Garren & Strauss, 2009) or plant survivorship (e.g. Ortega et al., 2012) by increasing seed germination, seedling survivorship per unit area or the reproductive potential of survivors such that the net reproductive rate remains unchanged or is even increased. Thus, biological control agents can harm individual plant fitness but sometimes fail to reduce densities or seed production per unit area for the target plant.

3. Biological control agents and community and ecosystem dynamics

Target plant populations are nested within a community matrix that also affects seedling survivorship and plant reproductive
output, and these impacts can be independent of biological control impacts. Thus, the outcome of a specific seed or plant mortality rate becomes context or habitat specific. For example, Fig. 3 shows that a reduction in seed production from level 'A' to level 'B' has no effect on target plant densities in habitat 1, but reduces densities to c. 50% of maximum values under conditions envisioned for habitat 2. Increased seed predation may in theory allow for increased seedling survivorship, but that survivorship is constrained by factors such as plant competition for seed safe sites and resources for seedlings, or the positive and negative feedbacks provided by the soil microbial community. Similarly, increased mortality rates in adults, leading to lower survivorship and reduced longevity, may not lead to increased growth or seed production of surviving plants if abiotic resource constraints, alone or in combination with plant competition, prevent a compensatory response at the individual level.

Each community brings factors controlling the population dynamics of the invasive plant that are potentially independent of the biological control agent, but can affect the efficacy of the interaction. In particular, the feedbacks from soil microbes often differentially affect plant fitness (Bever, 2003; Yang et al., 2013; Maron et al., 2014), as can the differences caused by a different plant community (Sun et al., 2014). The presence or absence of endophytes in two or more habitats may also influence these outcomes (Saikkonen et al., 1998). Endophytes often affect herbivores (Backman & Sikora, 2008), in addition to directly altering plant competition outcomes (Aschehoug et al., 2012) which again can affect plant responses to herbivores as shown in Fig. 2. The presence or absence of mycorrhizal fungi can also impact herbivore responses (Hartley & Gange, 2009), and the presence or absence of other herbivores and pathogens can affect plant performance and competitive interactions with other plant species (Borer et al., 2007; Perkins & Nowak, 2012; Hauser et al., 2013). Thus, the extent of control is not just about whether the right biological control agent was selected. Rather, it is how the biological control agent functions under the new conditions generated in the introduced environment that determines the net effect of control by top-down factors, including the control contributed by the biological control agents.

The introduced habitat of an invasive species has specific climate, resource, and disturbance regimes that can directly affect the efficacy of biological control (Fig. 2). Temperature, moisture, nutrients, and fire affect the fitness of both the biological control agents and the target species; responses are potentially independent. Such abiotic factors also indirectly influence the interaction via their controls and impacts on other components of the biological community. As these abiotic drivers are now undergoing directional changes in many regions, specific examples of abiotic effects on biological control agents are deferred to the discussion of these changes in Section IV.6 below.

4. Improving the efficacy of biological control agents

Invasive plants have been a focus of population- and landscape-level modeling efforts for decades (e.g. Rejmánek & Richardson, 1996; Parker et al., 2001), and using models to evaluate biological control efforts is now an active area of research (Buckley et al., 2004; Shea et al., 2010; Swope & Satterthwaite, 2012; Yeates et al., 2012). Modeling approaches are deemed valuable both in predicting potential biological control outcomes and in post-release assessments of impacts on densities and distributions of target plant species. Spatial modeling demonstrates that the spread of a plant species can be related to demographic factors (Jongejans et al., 2008, 2011) and, importantly, these models indicate that the impacts of biological controls include the rate of dispersal via multiple effects on seed numbers and characteristics, as shown in nodding thistle (Marchetto et al., 2014).

In theory, the testing of agents before release greatly reduces the number of undesirable outcomes and increases the probability of control. Nonetheless, expecting a very high percentage of successes seems unrealistic. That said, characteristics or traits of both the control agents and the target species have now been identified that may facilitate identifying effective biological control agents (Clewley et al., 2012; Paynter et al., 2012; Pearse & Altermatt, 2013), and lessons learned from the past should facilitate a higher success rate in the future.

The Müller-Schärer & Schroeder (1993) report identified a number of issues related to biological control that have remained major research concerns. First, they identified the fact that revegetation is often required to prevent one weed from replacing another. These observations have been verified numerous times since that report (e.g. Cutting & Hough-Goldstein, 2013; Van Driesche & Center, 2014). Changing a grazing regime could facilitate the biological control activity or even eliminate the need for specialist biological control agents. Knapweed and many other invasive forb species in North America could be controlled by switching from grazing by cattle to grazing by sheep and goats, but such an activity is deemed socially or economically unacceptable by stakeholders (Alper, 2004).

Cumulative stress to target plant species also involves decisions regarding the numbers and modes of damage caused by herbivores and pathogens. McEvoy & Coombs (2000) and Denoth et al. (2002) emphasized that, along with potential benefits, each
biological control agent brings its own risk. The large number of insect species released against the knapweeds in North America was used as an example of problems that generated a large number of unintended consequences while not solving the initial problem (Louda & Stiling, 2004). The successes eventually observed for the knapweeds required that the multiple species of biocontrol agents produced additive effects (cumulative stress) that suppressed plant fitness to levels affecting the plants’ abundance in the introduced community (Knochel et al., 2010; Stephens & Myers, 2014). These successes reduced densities of the target species to levels where the unintended consequences of the ineffective biological control agents either disappeared or were greatly diminished as a result of their own numerical declines.

Biological control agents can exhibit antagonistic effects with other biological control agents that reduce their efficacy (e.g. Crowe & Bouchier, 2006; Milbrath & Nechols, 2014). For nodding thistle (case 3), the efficacy of a superior biological control agent was shown to be reduced by the presence of an inferior biological control agent (the notorious R. conicus) using both modeling and empirical findings (Shea et al., 2005; Groenteman et al., 2007). Stephens et al. (2013) conducted a meta-analysis of studies reporting results of antagonistic, additive or multiplicative effects when multiple species of biological control agents were used on target plants. They found that, in about one-quarter of 51 studies reviewed, impacts were reduced as a result of antagonistic interactions, whereas three-fourths of the studies showed that insects had cumulative or independent impacts on target plants. They emphasized the simple rule that programs should avoid introducing species that attack the same part of the plant at the same time.

5. Rapid evolution contributes to how target plants respond to biological control agents

Invasive plants often exhibit growth traits and competitive interactions that are markedly different in the introduced habitat than in their native habitat, and these differences have been attributed to ecosystem and community changes, as described in Section IV.3 above. The genetic composition of the target species also influences these observed differences among habitats (e.g. Blossey & Nötzold, 1995; Sakai et al., 2001). The process of preadaptation and evolution of invasive plants and biological control agents during the invasion process remains poorly understood (Marsico et al., 2010). Natural selection appears to operate very rapidly on introduced species (e.g. Sax et al., 2007; Turner et al., 2014) as well as the biological control agents released on these species (Hufbauer & Roderick, 2005; McEvoy et al., 2012). Tamarisk shrubs and trees, the plants discussed in case study 1, are genetically different in their introduced and native ranges (Sher, 2013) and the biological control insects have also evolved new diapause strategies in the introduced habitat (Bean et al., 2012). Rapid evolution of control agents can be caused by changes in the phenology, chemistry and growth characteristics of the target plant, but also by potential differences in the introduced environment (McEvoy et al., 2012). While the invasive plant may be relatively new to the introduced community, we should expect a variety of changes, including those described as ‘community-based coevolution’ (Straus & Irwin, 2004), and the combination of herbivores and pathogens already present in the community, in conjunction with the biological control agents, will affect both the target plant species and the overall community organization (Ohgushi, 2005). While rapid evolution in diet breadth of biological control agents has not been identified as a problem, McEvoy et al. (2012) advocate evaluating the evolutionary potential of biological control organisms before their release in new environments and provide criteria for that evaluation.

6. Global environmental change drivers alter abiotic and biotic controls

Global change drivers, such as elevated CO2, climate warming, and nitrogen deposition, have important direct and indirect effects on ecological interactions among insect herbivores and their host plants (Throop & Lerdau, 2004; Jamieson et al., 2012b; Robinson et al., 2012). Accordingly, these factors may alter the effects of insect biocontrol agents on target plants, potentially creating challenges for evaluating biological control programs. The effects of growing season duration in addition to temperature changes may also impact biological control efforts. Insects may adjust diapause durations to adapt to the timing and length of the host growing season (Bean et al., 2012). At least a subset of biological control agents may be capable of increasing the number of generations produced per year as the growing season lengthens. An example is the picture-winged flies (Urophora spp., Tephritidae) released against knapweeds. When attacking a target species, these species show a single generation in colder regions, but can have up to four generations in warm temperate zones (Duguma et al., 2009). As growing seasons expand, at least some portion of the biological control agents will be able to exploit this increase by increasing the number of generations produced per growing season. Finally, differential species responses to warming can alter phenological synchrony between insects and their host plants (e.g. Schwartzberg et al., 2014), potentially affecting insect performance, plant damage, and population dynamics of interacting species.

Biological control impacts on plants can be magnified or attenuated by climate (Thompson et al., 2010; Maines et al., 2013). Dodder, if the duration (case 3) alters the timing of its growth dynamics across its introduced range, altering the impact of biological control agents (Cullen & Sheppard, 2012). Similarly, interpretations of the efficacy of the biological control agents can be confounded by climatic factors (Sims-Chilton et al., 2010). Directional changes in climate and resources, and ongoing changes in the composition of the introduced community further confound biological control outcomes. The composition and strengths of interactions generated by the biotic components of a plant community (e.g. Fig. 2) are changing. Invasive plants in many parts of the world are now found in plant communities that have experienced directional change drivers in terms of the amounts and seasonality of precipitation (e.g. Prevéy & Seastedt, 2014) and growing season duration (e.g. CaraDonna et al., 2014). Carbon dioxide fertilization appears to differentially affect plant species, with many invasive plants showing disproportionately large positive responses.
to increased carbon dioxide (Ziska, 2003). Changes in plant water use efficiency in response to increased carbon dioxide concentrations clearly benefit some invasive plants (Blumenthal et al., 2013). The growth responses to increased carbon dioxide may also influence plant nitrogen content, which can be a major control over herbivory (Fajer et al., 1989). Meanwhile, higher amounts of plant-available nitrogen in the atmosphere as a consequence of human activities influence herbivory directly (Throop & Lerdau, 2004; Throop, 2005) but also affect plant competitive interactions and diversity (Duprè et al., 2010). Finally, changes in disturbance frequencies such as fire intervals (Liu et al., 2013) or extreme weather events (Díez et al., 2012) can favor a subset of plant species, including invasive species. Understanding and managing invasive plant species require an understanding of how these collective and interactive changes are affecting the introduced species and their biological control agents.

V. Social dimensions of biological control

1. Communications of scientists with managers: monitoring the outcomes

Monitoring of management outcomes of invasive plant control strategies remains a neglected and underutilized activity (Maron et al., 2010; Martin & Blossey, 2013). Follow-up assessments of biological control releases and their impacts are relatively few compared with the overall volume of literature on biological control research (Clewley et al., 2012). The societal relevance of these efforts makes biological control monitoring an unexploited educational and outreach opportunity; they also make for interesting citizen science projects (Weed & Schwarzländer, 2014). Mapping distributions of invasive plants on an annual basis is often a land manager’s mission. Managers often know where the invasive plant species are, but they seem less aware of the presence and status of biological control agents on these species. Land managers need to participate in and expedite approved biological control releases, but also need to maintain target plant populations as refugia for the biological control agents while the control process is developing. These science-to-practice communication failures relate to the culture of information transfer, at least in the USA (Matzek et al., 2014). The process could be greatly improved by having scientists embedded in management programs (Chapin et al., 2010) and both monitoring and modeling efforts involving scientists, educators, and managers might be particularly productive. Overall, the application of biological control appears to be proceeding more slowly than one might expect based upon its scientific and economic benefits (Shaw et al., 2010).

2. Invasive species as ‘wicked problems’

Chapin et al. (2008) described environmental problems whose impacts vary across spatial scales, and across socio-economic, cultural and ecological domains, and that affect stakeholders differentially, as ‘wicked problems’. The uncertainty about future conditions and differences in social values associated with conservation efforts make it impossible to define an optimal solution (Shindler & Cramer, 1999). With every ‘solution’ comes a new set of ecological and economic issues. If invasive species are wicked problems, then the wicked solutions, including biological controls, come with their own set of ecological, economic and social consequences. While a majority of stakeholders may agree that an introduced plant species may have undesirable effects, the decision to invest large amounts of time and funding to either eradicate or effectively control the species is less certain.

Among the strong advocates of biological control are those that prefer any alternative to herbicides, in part because of documented past impacts and abuses of pesticides, and in part because of concerns about undocumented effects or synergisms with other chemicals in the environment. This group is focused primarily on the wellness dimension of human well-being, perhaps for good reason, but also on the documented nontarget effects that herbicides have on native plants. At the same time, some conservationists abhor the introduction of additional, nonnative species to control invasive plants, because, primarily, of fears of what might happen. The cautionary tale of the release of Rhinocyllus conicus is often invoked. Current procedures would preclude the release of this insect, but it often remains the ‘poster-child’ for ongoing discussions of biological control agent risks. The accidental release in North America of the biological control agent that solved Australia’s cactus invasion, the moth Cactoblastus cactorum (Pyralidae), provides another discussion point against biological control. Here, the release was apparently accidental but the harm to native cacti is large (Suckling & Sforza, 2014). Finally, the possibility that rapid evolution might produce unanticipated host shifts or other nontarget effects, while not documented to date, remains an ongoing discussion and research topic (e.g. McEvoy et al., 2012).

Scientists can act as ‘profilers’, and species that have recently arrived in biotic communities (aka ‘aliens’) are ‘immediate suspects’ because of probabilities of impacts. Others might label this xenophobia as the current expectation is that the consequences of most plant species introductions will be minimal. While most scientists may not be xenophobes, 20 yr of interactions with stakeholders and managers convinces me that xenophobia is a factor contributing to the invasive species ‘wicked problem’, and this xenophobia carries over to biological control agents as well. A solution for future invasions by plants is to agree that early detection and eradication of introduced species is the best policy (Shackelford et al., 2013), and such a policy, if successful, would mean that we would only have to deal with the current suite of regionally abundant introduced plant species, a sufficiently daunting task.

The scientific community continues to differ on the relative benefits and threats posed by biological control agents. Suckling & Sforza (2014) developed a risk management framework for biological control agents and found that >99% of over 500 agents had no significant adverse effects. The authors believed that, given improved safety procedures in recent years, even fewer unintended consequences from deliberate releases should be anticipated in the future. Nonetheless, Simberloff (2012, p. 263) stated, ‘Despite prominent examples in both the general invasion literature and that for biological control, the risk that a species, once introduced, will spread beyond its intended range, and the consequences of such
spread, are not routinely treated by risk assessors’. Further, the use of biological control assumes the target plant cannot be eradicated, a fact that puts limits on restoration goals. Hence managers committed to classical restoration approaches must, by definition, at least lament the use of biological control agents. If one acknowledges that increased rates of environmental change across the planet are real and being influenced by human activities, then ‘controlled change’ and ‘uncontrolled change’ drive the future conditions of our ecosystems. Stakeholders and managers must therefore choose between the two scenarios. If that is true, then, when sustainable reductions in regionally abundant invasive plants are identified as management goals, biological control should receive strong support from scientists, managers, and stakeholders.

As human alterations of the planet continue, both the absolute and relative ecosystem services of a recently introduced plant change through time. Plant species initially introduced into new habitats but later found to be unacceptable (e.g. species of tamarisk discussed in the first case study) or accidentally introduced and invasive (e.g. the knapweeds or nodding thistles in the second and third case studies) can subsequently be revalued by stakeholders. Tamarisk now provides essential habitat for a desirable and rare species and cost-effective solutions to erosion control (Sher, 2013) and the species of introduced asters provide a food source for critically needed pollinators as well as a food industry (Carson, 2013). Substantial reductions in these plant densities clearly have their own unintended consequences (Zavaleta et al., 2001).

VI. The future for the application of biological control of plant invasions

The procedures for identification of invasive plants that are suitable and appropriate for biological control efforts are improving (Jongejans et al., 2006; Paynter et al., 2012; Blackburn et al., 2014). In spite of the current factors contributing to uncertainty and the community-specific responses expected to impact the efficacy of any single biological control agent, the track record for the current suite of biological control releases on invasive plants is very good. Recent summaries by Cullen et al. (2011) and Julien et al. (2012) provide impressive accounts of the biological control programs in Australia, and provide commentary and insights on successes and failures. This record may never be excellent, but it can be better (Morin et al., 2009; Fowler et al., 2012). Successful biological control programs require buy-ins from policy makers, scientists, managers, and stakeholders, and no ‘one size fits all’ biological control program exists. However, in South Africa, a country with invasive plant species problems that have very large economic and ecological dimensions, comprehensive programs have been developed that can empower current and future biological control initiatives (e.g. van Wilgen et al., 2004, 2011, 2013).

A tenet of ecosystem management and, more recently, ecosystem stewardship is to ‘expect surprises’ (Chapin et al., 2010; e.g. Fig. 4). How the magnitude and direction of global environmental change drivers are going to impact and be impacted by community food webs remains uncertain (Tylianakis et al., 2008). Adding a non-coevolved plant species to a community clearly can cause major restructuring of the community even in the absence of other environmental changes, and new combinations of abiotic and biotic factors will produce new invasive plant distributions (Bellard et al., 2013) and novel ecosystems (Hobbs et al., 2014). Surprises have happened and will continue to happen with the application of biological control agents. With the amount of current and future human travel and commerce essentially linking all continents, increases in the introduction of plants as well as accidental introductions of herbivores and pathogens that will function as both pests and biological control agents are likely (e.g. Sullivan, 2014). To date, only a few biological control agents have been discovered where they are very much unwanted and represent both ecological and economic problems (Zimmermann et al., 2000), but other biocontrol agents have been found great distances from approved release areas (Pratt & Center, 2012).

Davis et al. (2005) make the argument that invasion biology needs to be nested in a larger theoretical framework of plant community ecology that accommodates abiotic and biotic changes as both natural (e.g. classic succession) and anthropogenic (e.g. global change driver) phenomena. Thus, grassland invasions by native or nonnative trees would be treated under the same conceptual framework. Forest die-back caused by native or introduced insects and pathogens would be treated similarly. Studying biological control of plant invasions as if the environment surrounding this system is static is necessary but not sufficient, and invasion science needs to be multidisciplinary (Richardson, 2011). Plant invasions have been identified both as causes and as consequences of global environmental change, but impacts of these plants are often generated by the interactions with human disturbances and other global change drivers (Blumenthal et al.,...
2013; Prevèy & Seastedt, 2014). Because decisions to use biological control are driven by the assessment of these impacts, an integrated, interdisciplinary, and proactive approach to the science is warranted. Further, the science needs to acknowledge that biotic feedbacks to the earth climate system are contributing to the structure and function of future ecosystems (Knight & Harrison, 2013). While climate change, atmospheric chemistry, changes in disturbance frequencies, and extreme events are affecting biotic communities, the communities are interacting with, not just reacting to, these changes. Accordingly, the science of plant invasions and the application of biological control to maximize ecosystem services and conservation values are appropriate topics to be nested within ecosystem stewardship and sustainability science programs (Chapin et al., 2010).

A real concern for the 21st Century is that rapid environmental change will require ecosystem managers and conservationists to practice triage activities. Introduced species and biological control agents will eventually factor into this process, and both are likely to be important as these scenarios progress (van Wilgen et al., 2013). Unless we relegate certain plant species to botanical gardens, we may not be far away from recognizing that species migrations and assisted colonization (i.e. the deliberate movement of species to areas previously not occupied by those species) are the only solutions for the persistence of a subset of plant species (Hancock & Gallagher, 2014). When that day comes, arguments related to ‘native’ and ‘nonnative’ status of species become moot (but see Webber & Scott, 2012). Regardless, economic and ecological concerns about invasive plant species will continue. As Suckling & Sforza (2014) emphasize, risk needs to be assessed in terms of undertaking a management action as opposed to the risk of not taking that action, or relative to the risks and costs of alternative actions. A key challenge is to quantify the risk of proactive management versus no management under the changing conditions currently experienced and anticipated in the near future. Strategic approaches that recognize the social, economic, and ecological dimensions of the problems are available (e.g. van Wilgen et al., 2011), and these are the model systems that provide a way forward. Admittedly, biological control programs must continue to be a species-by-species endeavor. When invasive plants clearly impinge directly and indirectly upon human well-being, biological control programs remain cost-effective and sustainable tools to be used to maintain or enhance ecosystem services and conservation values. Such activities should receive strong consensus and funding mandates.

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